Journal of Phycology
August 2021, Volume 57, Issue 4, Pages 1140-1150
https://doi.org/10.1111/jpy.13162
https://archimer.ifremer.fr/doc/00683/79498/

Range extension of mesophotic kelps (Ochrophyta: Laminariales and Tilopteridales) in the central north Atlantic: Opportunities for marine forests research and conservation

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Abstract :

Kelp was first recorded for the remote warm-temperate Azores archipelago (central North Atlantic) as late as 1971, when a few Laminaria specimens were collected on the Formigas Bank at depths beyond conventional SCUBA diving reach. A shortage of technical means and projects targeting mesophotic environments has since kept this offshore marine protected area as the single known kelp occurrence site. Here, we present new kelp records collected on previously unexplored mesophotic reefs using remote imaging systems, open and closed-circuit SCUBA diving and fisheries by-catch information. The new data extends the known distribution range of kelp in the Azores 350 km to the west and 25 km to the southwest, henceforth including several island shelves in eastern and central Azores. In addition to the previously recorded Laminaria ochroleuca, kelp specimens with a morphology akin to Phyllariopsis brevipes subsp. brevipes are also reported. For the first time, seabed imagery is used to document the depth-wise diversity of the Azores kelp beds and their associated biota. Our findings emphasize the poor knowledge that persists in regard to Macaronesia's mesophotic environments located beyond conventional SCUBA diving limits. The new on-shelf kelp occurrences add conservation value to coastal areas and should facilitate island-based research. However, their greater proximity to land-based impacts and exposure to climate change also raise management needs.

Keywords : associated biota, Azores, deep-water, kelp, Laminaria ochroleuca, marine forests, Phyllariopsis brevipes subsp. brevipes, range extension

List of abbreviations: DDC - drop-down camera, LEK - local ecological knowledge, ROV - remote operated vehicle, SST – sea surface temperature

INTRODUCTION

Kelps are large brown macroalgae that play a major ecological role as sessile primary producers and habitat-building species. Their canopies support a variety of associated biota that form complex food webs and enhance secondary productivity (e.g., Steneck et al. 2002, Araújo et al. 2016). They are found worldwide in intertidal and infralittoral rocky substrates in temperate to sub-polar coastal ecosystems. However, as average surface seawater temperature increases towards lower latitudes, the niche occupied by kelps is generally displaced towards deeper euphotic levels in a classic example of 'equatorial' or 'isothermic submergence' (Lüning 1990).

As suggested by Graham et al. (2007), low-latitude refuges occur in an abiotic belt ranging from (i) an upper limit determined by surface waters that are permanently or seasonally too warm for kelp recruitment and survival to (ii) a lower limit determined by the kelps' photosynthetic compensation depth, where solar irradiance becomes insufficient to meet their phototrophic requirements. Horizontally, the niche of low-latitude kelps would be constrained by substrate and nutrient availability with populations thriving in rocky areas subject to topographical or wind-induced upwelling.

In warm-temperate to subtropical oligotrophic parts of the northeast Atlantic, these ecological conditions mostly occur low in the infralittoral (sensu Hiscock and Mitchell 1980) or high in the mesophotic (sensu Hinderstein et al. 2010 with Kahng et al.'s 2010 extension of the concept to higher latitudes). Correspondingly, kelps have been recorded at depths ranging from 20 to 120 m in the Mediterranean Sea (see review in Flores-Moya 2012), the Macaronesian archipelagos (Tittley et al. 2001, Haroun et al. 2002, Fundação Rebikoff-Niggeler 2020) and shallow seamount tops off southwestern Iberia (e.g., Tittley et al. 2014).

A checklist of Macaronesian kelp records validated by recent literature (Tittley et al. 2001, Haroun et al. 2002, Tittley et al. 2014, Gallardo et al. 2016) yields a mere two native occurrences (*Laminaria ochroleuca* and *Saccorhiza polyschides)* and an introduced species (*Undaria pinnatifida*; see Fig. 1 A for validated records and Table S1 in the Supporting Information for complete historical checklist). Beyond these floristic records, only Ramos et al. (2016) provided image-based insight into the biota associated with Gorringe Bank's kelp beds and their variation with depth. Finally, the role of mesophotic reefs in Macaronesian offshore seamounts and archipelagos as climatic refuges for certain kelp species and their genetic diversity was brought to light by Assis et al. (2016, 2018).

Azores

Kelp specimens were first collected in the Azores archipelago (warm temperate mid-north Atlantic) as late as 1971 (Ardré et al. 1973), when the French expedition *BIAÇORES* visited the isolated Formigas bank. Ten years later, the Dutch expedition *CANCAP-V* confirmed the occurrence of *Laminaria* when dredging at 43-45 m depth on the same isolated seamount top. In the early 1990's, the University of the Azores sampled near the Formigas Islets (Neto et al. 2020) with SCUBA divers collecting kelp specimens that, together with the specimens from *CANCAP-V*, were used to formally record *L. ochroleuca* for the Azores (Tittley et al. 2001).

With no other records stemming from the preceding century-long surveying effort, kelps in the Azores remained an understudied peculiarity of the remote Formigas Bank. The shortage of remote imaging platforms until the mid 2000's and a community of phycologists focusing on more accessible coastal environments hindered further studies.

Nearly five decades after the first record, we document new kelp occurrences from surveys made between 2002 and 2018 throughout the archipelago using remote imaging systems, open and closed-circuit SCUBA technology and scientific fishery cruise bycatch records. Imagery is used to illustrate the Azores kelps and provide the first insight into the depth variation in the associated biota. In view of the updated distribution of mesophotic kelps, we discuss emerging conservation needs and research opportunities.

MATERIALS AND METHODS

Study area

The Azores is an archipelago located approximately 1600 km to the west of mainland Portugal (Fig. 1A) and 1900 km to the southeast of Newfoundland. Its nine inhabited islands spread across the Mid-Atlantic Ridge between 37º and 40º N and 25º to 32º W. Biogeographically, the Azores are in the Macaronesia region, which includes the other North Atlantic warm temperate to subtropical archipelagos of Madeira, Salvage and the Canary Islands. Tittley and Neto (2006) have shown the Azores marine flora exhibits a very low endemicity with species from both sides of the Atlantic. Although the geometry of the affinities varies slightly across Chlorophyta, Rhodophyta, and Ochrophyta, the closest floras are those of the other Macaronesian archipelagos, the Atlantic coasts of the Iberian Peninsula (temperate Northeast Atlantic) and, to a lesser degree, of the Carolinas' coast (northwest Atlantic).

Because of their volcanic origin and relatively young age, the Azores islands exhibit very narrow island shelves ranging from 140 m to 4 km width (Tempera 2008), with the adjoining island flanks dropping steeply to depths averaging 2000 m. The topographically-rich Azores Plateau features also 400 seamounts (Morato et al. 2008) of which only three (Princess Alice, Dom João de Castro and Formigas) have summits that rise up to the euphotic zone. Overall, the Azores infralittoral grounds are estimated to occupy a mere 895 km^2 (Amorim et al. 2015).

The Azores region is bound between two eastward currents branching from the Gulf Stream. Confluence conditions determine that in the vicinity of the islands the far-field vorticity is largely dissipated or broken down into smaller eddies (further details in Caldeira and Reis 2017). Therefore, the main hydrodynamic forces impinging on the island shelves are the prevailing swells from W to NW, which exhibit average significant wave heights exceeding 2 m (Rusu and Guedes Soares 2012), and the currents induced by microtides with a maximum astronomical range of 1.5 m (Instituto Hidrográfico 2005).

Sea-surface temperature (SST) exhibits large-scale spatial and seasonal variation (Lafon et al. 2004), ranging from 16 to 24ºC (Caldeira and Reis 2017). During winter, mixed conditions prevail in the upper ocean down to 150 m depth. Surface stratification develops during the summer with a thermocline occurring between 40 and 100 m depth (Santos et al. 1995). Surface waters in the region are generally oligotrophic (Santos et al. 1995) but nutrient-rich sub-thermocline waters can locally upwell into the euphotic zone as a result of frontal, topographical or vorticity effects, subsequently stimulating primary production.

Benthic surveys

Sublittoral kelp occurrence was investigated across the Azores by targeting rocky and mixed seabed areas between 35 and 85 m depth, which generally corresponds to the habitat requirements observed on Formigas. The surveys were performed between 2004 and 2018 using: (i) two small remote operated vehicles (a VideoRay Explorer micro-ROV and a SeaBotix LBV300S-6 mini-ROV); (ii) two custom-made drop-down cameras (or DDCs) built from Tritech MD4000, GoPro Hero3+ and GitUp Git 2 cameras; and (iii) SCUBA diving using conventional open-circuit systems for dives shallower than 40 m and rebreathers (RB80 Passive Semi-Closed, JJ Closed-Circuit and Sidewinder sidemount rebreathers) for deeper dives. A few specimens by-caught in the course of the ARQDAÇO fisheries surveys organized by IMAR/DOP-University of the Azores were also included in our record list.

ROV deployments were essentially point dives conducted while the boat was at anchor and observations could be approximately positioned using a surface GPS. A 2-3 kg drop-weight was attached to the tether 11 m away from the ROV to minimize current-induced drifts and dampen swell movements. The observations conducted at each station were generally restricted to this radius around the drop-weight.

DDC deployments generally consisted of transects ranging between 5 and 40 min or, when current drift was insufficient to provide a fast enough drift over the seabed, multiple point drops done parallel to the depth gradient.

SCUBA diving was used both to collect specimens in locations of attested kelp occurrence and, in the case of dives with rebreathers, to collect seafloor video in depths between 42 and 80 m.

ROV and DDC deployments were conducted mostly during daytime apart from a few exploratory night-time deployments aimed at investigating the occurrence of particular nocturnal fauna. To maximize the inventory of kelp-associated species, the understory stratum was also explored as much as practicable with the ROVs and DDCs. Kelp specimens and blade fragments collected by divers or by-caught by fishing gear and vessel anchors were used to identify associated epiphytes.

Overall, the imagery compilation used in this study comprised 36 hours 48 min of video footage and 59 still photos of kelp habitat. The duration of the video footage per island/bank is presented in Table S2 in the Supporting Information.

Complementary local ecological knowledge (LEK) on kelp occurrence, location, seasonality and perceived abundance trend was sought from local regular sea users. The original interview form, which covered a broader range of marine biotopes and species of conservation and scientific interest, is shown in Appendix S1 in the Supporting Information. Between 2016 and 2018, 30 interviews were conducted with professional and recreational fishermen, spearfishers, harvesters, sea tourism operators, dive masters and SCUBA divers on the islands of Corvo, Flores, Graciosa and Santa Maria. The permits to interview human subjects were issued by the Azores Regional Government Directorate for Sea Affairs in the scope of the MoniZec-ARP project.

Video annotation

Given the heterogeneity of the imagery originating from different ROVs, DDCs and SCUBA divers in terms of scaling, orientation and quality, annotation followed a simple protocol focusing on determining kelp occurrence, compiling a general list of visually identifiable associated taxa and interpreting bionomical changes throughout the kelps' depth range.

Remote imaging systems were deployed without any underwater positioning system. Annotations from ROV and DDC point deployments from vessels at anchor were thus given single geographic positions corresponding to the average vessel GPS coordinates. In the case of DDC drift transect annotations, coordinates were estimated for every 20 s video section by interpolating boat positions. A correction was introduced where possible for the layback between the boat and the camera's position on the bottom.

Taxonomical identifications were based on the expertise of the senior authors (F. Tempera, D. Milla-Figueras and P. Afonso), who have been conducting underwater surveys in the Azores and taxonomical work on coastal macroalgae, macroinvertebrates and fish for one to two decades. Imagery annotation was further supported by illustrated marine life guides for Macaronesia and North Atlantic (e.g., Cabioc'h et al. 1992 and Neto et al. 2005 for macroalgae; Wirtz 1995 and Wirtz and Debelius 2003 for invertebrates; Debelius 1997 for fish). In the lab, more specific taxonomical works were consulted when necessary.

RESULTS

Distribution

The geographical distribution of kelp occurrences (presences and absences) identified by the sampling effort is shown in Figure 1, B and C. Readers interested in the geospatial information and respective metadata are referred to the EUROBIS dataset (DOI: 10.14284/423; Tempera et al. 2020). In addition to the previously-known occurrence of *Laminaria ochroleuca* on the Formigas Bank (located in the eastern-most part of the Azores archipelago), three new areas have been identified on the island shelves of Santa Maria, Terceira and Graciosa islands. A timeline of the data collection progress across the archipelago is presented in Table S3 in the Supporting Information. The new occurrences extend the distribution range of the Azores kelps 353 km to the northwest and 25 km to the southwest, now encompassing both eastern and central Azores.

Occurrences ranged between depths of 31 m off the Graciosa northern shore to 84 m on Formigas shallow seamount summit. In terms of orientation, they largely clustered on north and northeast-facing shelf sectors, judging from the denser surveys made around Santa Maria and Graciosa. Marginal occurrences were located off Terceira's fully-exposed western shore and on leeside reefs off Graciosa's eastern shore. No occurrences were identified in southern-facing shelf sectors. Even in seemingly favorable sectors, presences were fairly patchy and did not form a continuous belt over suitable depths and substrates.

On the Formigas Bank, an offshore seamount summit fully exposed to ocean swells, dense kelp beds were detected on the Intermediate and Dollabarat reefs but only a few small kelp specimens were observed in the vicinity of the Formigas islets themselves.

Kelp were not detected in 22 rocky stations investigated on the Flores and Corvo shelves between 50 and 80 m depths, suggesting the species may be absent from western Azores. Similarly, kelp were not found on the shallow reefs that top the Princess Alice and the Dom João de Castro seamount summits.

Morpho-anatomy

Most kelp specimens observed match the typical *Laminaria ochroleuca* morphology, with flat broad blades, generally split into strap-like digits with a sizeable yellow patch at the base (Fig. 2, A-C). Stipes were stiff, cylindrical, smooth and devoid of epiphytes. Their holdfasts were formed by long branching haptera resembling a claw.

Specimens with entire or scarcely-split broad blades were observed on Formigas and off Santa Maria. The characteristic yellow patch was not always evident on elongated specimens with short stipes (Fig. 3, A-C) or in young specimens (Fig. 3D). However, the long split haptera characteristic of *L. ochroleuca* were still recognizable (Fig. 3, C and D) as well as white patches of the epiphytic bryozoan *Membranipora membranacea*.

Specimens similar in morphology to *Phyllariopsis brevipes* subsp. *brevipes* (order Tilopteridales, family Phyllariaceae) were observed on Formigas, Santa Maria and Graciosa from 43 m to 84 m depths. They presented entire or scarcely-split ovate translucent blades that were particularly elongated in certain specimens (Fig. 3, E and F). Their stipes were thin and short and merged into reniform or rounded blade bases (Fig. 3E). One specimen observed off Graciosa exhibited a discolored patch at the base of the blade that we interpreted as a sorus. This feature was placed very low on the blade and adjoined the blade margin as in *P. brevipes* subsp. *brevipes*. Lack of close-up footage prevented checking other *Phyllariopsis* diagnostic traits like holdfast morphology.

For reference, a list of the kelp specimens preserved in institutional collections is provided in Table S4 in the Supporting Information.

Kelp assemblages

A list of the 63 taxa identified in association with *Laminaria* and *Phyllariopsis* on the imagery or as epiphytes of the collected specimens is provided in Table S5 in the Supporting Information. Certain taxa are recorded above species level because imagery did not allow a more precise identification. Occurrences that could not be identified to at least order level were excluded, comprising several small rhodophytes and encrusting biota. Although inventories are provided per island/bank for detail, they should not to be considered equally exhaustive given variation in imaging platform, near-bottom operation and footage duration.

Profiles summarizing the species turnover observed along the kelps depth range per island/shallow bank are represented in Figure 4. Additionally, site-specific descriptions detailing variations in depth limits and associated biota are presented in Table S6 in the Supporting Information.

The shallowest *Laminaria ochroleuca* in the Azores were recorded at 31 m depth off Graciosa. They were part of a multispecific algal turf containing *Carpomitra costata*, *Dictyota dichotoma*, *Dictyopteris polypodioides*, *Halopteris filicina*, *Platoma* sp., *Sargassum* sp., *Sphaerococcus coronopifolius* and *Zonaria tournefortii,* as well as less prominent species such as non-geniculate coralline algae, *Peyssonnelia rubra*, and *Valonia* sp. Associated invertebrates included *Aglaophenia* sp., *Caryophyllia* sp., *Clavelina lepadiformis*, *Hermodice carunculata* and *Sabella spallanzanii*.

On the Formigas Bank, the shallowest kelp specimens were observed at 45 m depth among dense fronds of an elongated form of *Treptacantha* cf. *abies-marina* (which dominates the shallow reefs) and *Dictyopteris polypodioides*. At depths around 55 m, a dense canopy of *Laminaria* dominated the seabed with scattered tufts of *Carpomitra costata*, *Dictyopteris polypodioides*, *Sphaerococcus coronopifolius* and some *Phylariopsis* sp. observed on the canopy edges. Footage collected underneath the canopy showed an understory composed of rhodophytes (cf. Rhodymeniales), an Ulvaceae, *Halopteris filicina* and pennate hydroids (*Aglaophenia*, *Diphasia*). Rocky surfaces were colonized by encrusting biota including *Cutleria multifida* (Aglaozonia phase), non-geniculate coralline algae and unidentified sponges.

Off Santa Maria island, the shallowest *Laminaria ochroleuca* specimens were found at 46 m depth. They were accompanied by a dense turf of *Dictyopteris polypodioides*, *Sphaerococcus coronopifolius* and *Zonaria tournefortii.* As depth increased, *L. ochroleuca* became more abundant and dominant. Dense patches of *L. ochroleuca* were observed on rocks and rhodolith beds between

71 and 79 m depth (Fig. 3, A and B). Isolated specimens colonized cobbles scattered throughout neighboring patches of rippled biogenic sediment.

The deepest *Laminaria ochroleuca* stands were observed at 82 m depth on the Formigas Bank on a typical upper circalittoral setting with the underlying bedrock largely covered by oyster beds (likely *Neopycnodonte* and *Chama*) and the occasional *Centrostephanus longispinus*. Some elongated thalli with long split haptera, short stipes and long entire blades (which we tentatively identify as a form of *L. ochroleuca* growing outside the effect of wave action) were still observed on an exposed ridge at 84 m depth. They were accompanied by mesophotic corals (*Antipathella subpinnata*, *A. wollastoni*, and *Dendrophyllia* sp.), *Peyssonelia rubra* and a few tufts of filamentous red algae.

Colonies of the encrusting bryozoan *Membranipora membranacea* were observed on several *Laminaria ochroleuca* blades. This bryozoan was recognized by its kelp-fouling habit and its thin, pale-grey to white, smooth-edged encrustations with rectangular autozooids (Fig. S1F in the Supporting Information). Some fronds were also colonized by the hydrarian *Obelia* cf. *geniculata* which was recognized by its stolons with feathery stems bearing alternate polyps. This epiphyte was only discernible in by-caught specimens (Fig. S1E) or on close-up images with the blades at low angles.

Fourteen fish species were recorded in the kelp habitats (Table S5). Labrids, or wrasses, were the most diverse family with five species recorded. Rainbow wrasse *Coris julis* and blacktail comber *Serranus atricauda* were the most frequent encountered species.

DISCUSSION

Surveys of mesophotic reefs in the Azores show that kelps have a much broader distribution in this remote archipelago than previously known. Their geographical range is shown here to encompass not only the eastern-most euphotic reefs of the Azores (Formigas) but to extend well into central Azores. Rather than indicating a recent biological expansion, our 350 km range extension likely reflects increased surveying effort aimed at unexplored mesophotic reefs. Below we discuss taxonomical issues and various ecological and conservation implications stemming from the new observations. Emerging opportunities for nearshore kelp research are presented in Appendix S2 in the Supporting Information.

Taxonomy

Laminaria ochroleuca specimens exhibited a variety of frond types ranging from entire blades to more or less split blades (Figs. 2 and 3, A-D). Similar plasticity has been shown, for instance, in *L. abyssalis* (see Marins et al. 2012 and other cases cited therein). We relate the persistence of scarcely-split or entire blades in fully-grown *L. ochroleuca* to a lack of wave action in the deepest part of the species range. According to storm wave base estimates for the Azores (WB_{storm} = ½·Wave $Length_{perc-90}$), this mechanical effect should become negligeable below 64-66 m depth (Simões et al. 2010).

Observations of smaller kelp specimens with more delicate fronds suggest *Phyllariopsis brevipes* subsp. *brevipes* also occurs in the archipelago. Their morphology fits descriptions presented in Perez-Cirera et al. (1991) and Flores-Moya et al. (1993; see Results). Despite exhibiting particularly elongated blades (Fig. 3, E and F), none of the Azores specimens displayed lanceolate blades with cuneate bases like those of the *P. brevipes* subsp. *pseudopurpurascens* in Perez-Cirera et al. (1991). Our identification is further supported by the very low position of the sorus on the blade and that it nearly joins the blade margin, which further distinguishes it from *P. purpurascens*. We concur with Henry (1987)'s descriptions of *P. brevipes* subsp. *brevipes* growing on non-geniculate coralline algae (Fig. 3E) and occurring slightly deeper than *L. ochroleuca* (Flores-Moya 2012) to depths of several tens of meters (Flores-Moya et al. 1993). Considering the occurrence of *P. brevipes* subsp. *brevipes* in western Iberia, our records represent a 1600-km distribution range extension into the wider Atlantic.

We emphasize the fact that our observations are conservatively assigned to existing species based exclusively on morpho-anatomical characteristics. Microsatellite analyses by Assis et al. (2018) have previously shown a high level of differentiation of the Azores *Laminaria ochroleuca* that should be further investigated by DNA sequencing of existing samples (Table S4). This would not only settle the taxonomical status of the Azores populations but could also shed light on patterns of genetic diversity across the archipelago.

Isothermic submergence

The mesophotic niche of the Azores *Laminaria ochroleuca*, ranging 31 to 86 m depth, differs markedly from the situation found near its poleward range edge. In the western English Channel, for instance, the species occurs from low-water spring-tide levels to 25 m depth (Smirthwaite

2007). The concurrent equatorward sinking of depth limits and oceanic isotherms was originally named 'equatorial submergence' by Ekman (1953) and more accurately termed 'isothermic submergence' by Briggs et al. (1974). It has been highlighted in kelp by Druehl (1981) and Luning (1990) and likely reflects a critical intolerance to warm sea surface temperatures in one or more life stages (e.g., Izquierdo et al. 2002).

Graham et al. (2007) further related low-latitude kelp occurrence to cold nutrient-enriched niches created by upwelling. The concentration of our kelp observations on prominent seabed features such as island margins, shallow seamount summits and on-shelf reefs likely denotes similar conditions. However, further in situ environmental series and statistical analyses are required to validate oceanographic regimes and untangle the interplay of variables shaping the kelps' mesophotic niche.

Macaronesia's mesophotic belt

The novelty of describing mesophotic kelp beds emphasizes the enduring poor knowledge of the biological make-up of the Azores shelf habitats beyond conventional SCUBA depth limits. When compared to the short coralline and non-calcareous multispecific turfs that prevail to 40 m depth (Tittley and Neto 2000, Wallenstein et al. 2010), the kelp beds stand out for their three-dimensional structure and high biomass. This contrast emphasizes the mixed character of the biological zoning of Macaronesia's shelves and euphotic seamount tops, which combine temperate and tropical traits. As in temperate regions, altiphotic depths are dominated by algae, which in the Azores are generally kept relatively short by intense wave action. Below this level, low PAR attenuation produces a relatively-wide belt that matches the mesophotic zone described in oligotrophic tropical environments (see review in Spalding et al. 2019).

Associated biota

The sequence of biota observed in association with the Azores kelps along their depth range (31 to 85 m) suggests that their niche actually spans across the altiphotic-mesophotic transition (sensu Baldwin et al. 2018). On their shallowest reaches off Graciosa, kelps were accompanied by frondose Ochrophyta typical of well-lit depths (namely *Dictyota dichotoma* and *Treptacantha abies-marina*). Around 50 m depth, kelp stands comprised macroalgae with a deeper affinity such as *Carpomitra costata, Dictyopteris polypodioides*, *Phyllariopsis brevipes* subsp. *brevipes* and

Sphaerococcus coronopifolius). Finally, the deep *L. ochroleuca* observed below 80 m depth grew on rocks dominated by typical mesophotic fauna, namely oysters and sea urchins (*Centrostephanus longispinus* and *Echinus melo*).

Despite the three-dimensional framework provided by kelp, associated fish were not noticeably diverse or abundant, either above or below the canopy. This perception contrasts with the thriving fish assemblages we have encountered during fish counts in shallower reefs, notably on the Formigas Bank. While the depletion of fish assemblages towards mesophotic depths coincides with other studies (e.g., Brokovich et al. 2010), the particular prevalence of labrids is likely related to the abundance of frondose macroalgae (e.g., Tuya et al. 2009). Apart from the rare *Zeus faber,* the remaining fish species are all common in altiphotic habitats (Afonso et al. 2018). This suggests that the Azores mesophotic kelp stands are inhabited by broad-ranging non-specialist species (see Pyle et al. 2019 for a review of mesophotic fish biodiversity patterns).

Habitats that are comparable to the Azores kelp stands have been reported in other warm-temperate locations. The closest occurrence is on the Ormonde peak, a euphotic summit of the Gorringe seamount located 1200 km to the east of the Azores and 200 km WSW of the Iberian peninsula. The *Laminaria ochroleuca* depth range of 39 – 84 m reported there (Ramos et al. 2015) largely mirrors the Azores range of 31 – 86 m. Additionally, several matches can be found in the associated species. At both sites, the shallowest kelp occurrences are accompanied by *Dictyota dichotoma*, *Dictyopteris polypodioides*, *Zonaria tournefortii*, small rhodophytes, non-geniculate coralline algae and encrusting sponges (45-60 m). In the same way, kelp in 80 – 85 m depths were also found among circalittoral fauna, including *Antipathella subpinnata*, *Dendrophyllia* sp. and *Echinus melo*.

In the Mediterranean, *Laminaria ochroleuca* stands have been recorded in (i) the Alboran Sea (western Mediterranean), where the species thrives at depths between 30 and 50 m (Flores-Moya 2012), and (ii) the Strait of Messina (central Mediterranean), where the species reaches depths of 110 m (e.g., Fred and Giermann 1969). Off Brazil, Marins et al. (2014) have described *L. abyssalis*-rhodolith beds that resemble the *L. ochroleuca*-rhodolith association recorded off Santa Maria. In the latter two cases, rhodolith instability seems to expose tall specimens to toppling by strong currents, accounting for the predominance of small-sized specimens with short stipes.

Conservation interest

The Azores kelps are possibly the least studied in the Northeast Atlantic along with the *Laminaria ochroleuca* recently recorded off Madeira island (Fundação Rebikoff-Niggeler 2020). Although the geographical spread of our records decreases the Azores kelps vulnerability, several attributes continue to make them of conservation interest.

Assis et al. (2018) have already exposed the long-standing isolation of the Azores *L. ochroleuca* population and the role of Macaronesia's deep reefs as kelp refugia. The scattered and restricted distribution of the new records prompts further investigation into inter-island connectivity patterns and management measures that preserve them.

While benefitting from some buffering from natural and anthropogenic surface stressors, the mesophotic niche occupied by the Azores kelps remains nonetheless vulnerable to climate change. Projections by Assis et al. (2017) estimate that the thermal niche of *L. ochroleuca* in the archipelago should decline between 23% and 85% depending on the emission scenario retained (RCP 2.6 or RCP 8.5, respectively). We emphasize that the niche may be constricted simultaneously from above and below. Warmer, more stratified and nutrient-depleted ocean surface conditions (Capotondi et al. 2012) are expected to reduce the niche from the surface downwards (see e.g., Voerman et al. 2013 for *L. ochroleuca* range reduction on the Iberian shores). On the other hand, enhanced precipitation (Santos et al. 2004, Hernández et al. 2016) may result in increased siltation of island shelves and an attenuation of PAR levels that would diminish the kelps' niche from the lower depth limit upwards. Statistical modelling would be of use to identify environmental variables regulating the patchy realized niches observed on island shelves and seamount summits. The projection of these models using climate change scenarios would provide valuable insight into the maintenance of the kelps' niche and of their habitat-provisioning functions.

Altogether, the sources of vulnerability presented above call for precautionary management of kelp stands. Although the Formigas kelp population is already enclosed within a designated offshore site, this is not the case with the new kelp occurrences identified in the vicinity of inhabited islands. Their relative accessibility and limited regulation makes them susceptible to deliberate collection, especially where the kelp upper range is within reach of conventional SCUBA diving. Although seaweed harvesting using this practice is presently limited to depths above 10 m, this commercial activity is regaining momentum throughout the archipelago and has been traditionally important around islands such as Graciosa. Expanding existing marine protected areas to cover the most important kelp stands would better safeguard their integrity and associated ecosystem services.

Monitoring

The projection of a contracting niche should prompt a kelp monitoring program aimed at characterizing spatio-temporal patterns of abundance, demographical structure and recruitment. To boost the detectability of early-warning signs, marginal kelp occurrences should be targeted in parallel with dense stands. These efforts could benefit from the designation of a long-term ecological research (LTER) sites where time series would be acquired for key kelp-regulating variables such as temperature, PAR, hydrodynamics or herbivory pressure.

ACKNOWLEDGMENTS

This study was supported by the Portuguese Foundation for Science and Technology (FCT) through individual contracts and grants awarded to Fernando Tempera (SFRH/BD/12885/2003, SFRH/BPD/79801/2011) and Pedro Afonso (IF/01640/2015). EC project MARFOR (BIODIVERSA/004/2015) funded the work of David Milla-Figueras and part of the fieldwork. The 2018 campaign was further supported by project PLATMAR (FCT PTDC/GEO-GEO/0051/2014). The Azores Regional Government funded the BALA/MoniZec-ARP (DRAM) and MONIZEC2 monitoring programs which supported several surveys. Further thanks are due to the Oceano Azul Foundation and the Waitt Foundation for providing the opportunity and logistics to work off Flores and Corvo during the Blue Azores 2018 expedition. Renato Martins (IMAR-DOP/UAz) is acknowledged for all the hours spent operating and troubleshooting the mini-ROV *SP*. Dr. Richard Bates (University of St. Andrews, Scotland, UK) kindly provided the micro-ROV and camera used in the 2004 and 2005 surveys. Gonçalo Graça, Diya Das, the vessel crews of *Águas Vivas*, *Arquipélago* and *Nossa Senhora dos Milagres* were key to the success of several surveys. Todd Kincaid and Jarrod Jablonski (GUE/Project Baseline), Joana Boavida (UAlg), Pedro Ribeiro (Okeanos-UAz) and Valentina de Matos kindly shared metadata and video footage acquired during the Azores 2014 leg of project Baseline/Global Underwater Explorers. GreenPeace is thanked for inviting DOP-UAz researchers to their 2006 'Defending our Oceans' expedition in the Azores. Estibaliz Berecibar and Ester Serrão are thanked for guidance in identifying the *Phyllariopsis* specimens. Ricardo Serrão Santos and Frederico Cardigos generally supported and organized the first BANCOS expeditions promoted by IMAR/DOP-UAç. Anabela Simões and Manuela Juliano kindly shared wave statistics produced by the EasyCo project. Marina Carreiro-Silva (IMAR/DOP-UAz), Íris Sampaio (IMAR/DOP-UAz), Inês Tojeira (EMEPC), Manuela Parente (DB-UAz) and Judite Alves (MHNL-UL) are thanked for assisting with locating the Azores kelp specimens in reference collections. Amelia Curd is thanked for revising the English. Two anonymous referees are thanked for their insightful and meticulous suggestions, which have significantly improved this manuscript.

All research activities complied with marine protected areas regulations and legislation in place in the Azores (Portugal) concerning the collection of biological specimens and scientific study of vulnerable habitats (DLR 9/2012/A and DRR 20/2012/A). Interviews of human subjects were conducted under permits issued by the Azores Regional Government Directorate for Sea Affairs in the scope of the MoniZec-ARP project.

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Figure 1: A. Distribution of kelp species in Macaronesia. B. Location of the surveyed sites and *Laminaria ochroleuca* occurrences in the Azores archipelago (central North Atlantic). Detailed distribution of occurrences around Graciosa island (C), Santa Maria island (D) and the Formigas bank (E).

Figure 2: Diversity of the Azores *Laminaria ochroleuca* stands and specimens. A. Shallowest occurrence at 31 m depth within a *Dictyoperis polypodioides* facies (Graciosa island). B. Dense *L. ochroleuca* stand at 51 m depth (Santa Maria). C. Kelp occurrence at 80 m depth within circalittoral oyster facies (Formigas Bank). D, E, F. Specimens with different frond morphologies from Formigas, Graciosa and Santa Maria, respectively.

Figure 3: Specimens with entire or scarcely split blades. A, B. Small scarcely-split *Laminaria ochroleuca* fronds on rhodolith bed (Santa Maria, 72 m depth). C. Entire elongated *L. ochroleuca* frond displaying robust split haptera (Formigas Bank, 85 m depth). D Young *L. ochroleuca* (Graciosa island, 35-40 m depth). E, F. *Phylariopsis brevipes* subsp. *brevipes*. (E. Formigas Bank, 85 m depth, F. Graciosa island, 58 m depth).

Figure 4: Depth distribution of the kelp beds and associated biota at the different occurrence sites.

Figure S1: *Laminaria ochroleuca* frond details: A. Underwater appearance of fertile blade with sori (Graciosa island, 35-40 m). B. Cross section of blade with a sorus (from Terceira island, 35-40 m). C. Striated frond suggesting a damaged meristem or a peculiar senescence or soral morphology; D. Heavily-encrusted holdfast. E. Epiphytic hydrarian *Obelia* cf. *geniculata*. F. Epiphytic bryozoan *Membranipora membranacea*. (C to F, specimens from Formigas Bank, 55 m depth)

Table S1. Kelp species recorded in Macaronesia. Source: Algaebase followed by revision of recent checklists and a selection of original bibliography.

Table S2. Duration of video footage analyzed per island/bank.

Table S3. Sequence of records per site ordered from eastern to western Azores.

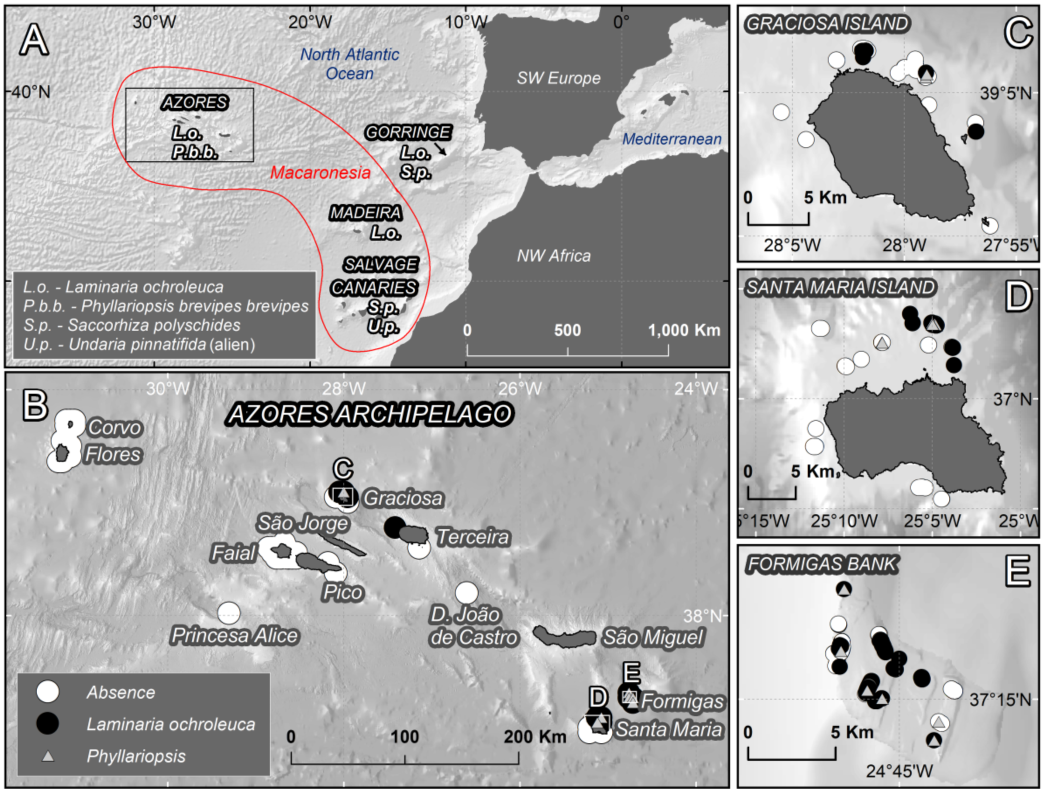
Table S4. List of Azores kelp specimens kept in reference collections

Table S5. List of species observed in association with the Azores kelps by phylum and detection method (V - video; S - SCUBA diving; B – longline by-catch)

Table S6. Description of the kelp assemblages from eastern to western Azores.

Appendix 1. Local Ecological Knowledge (LEK) interview form

Appendix 2 Future research



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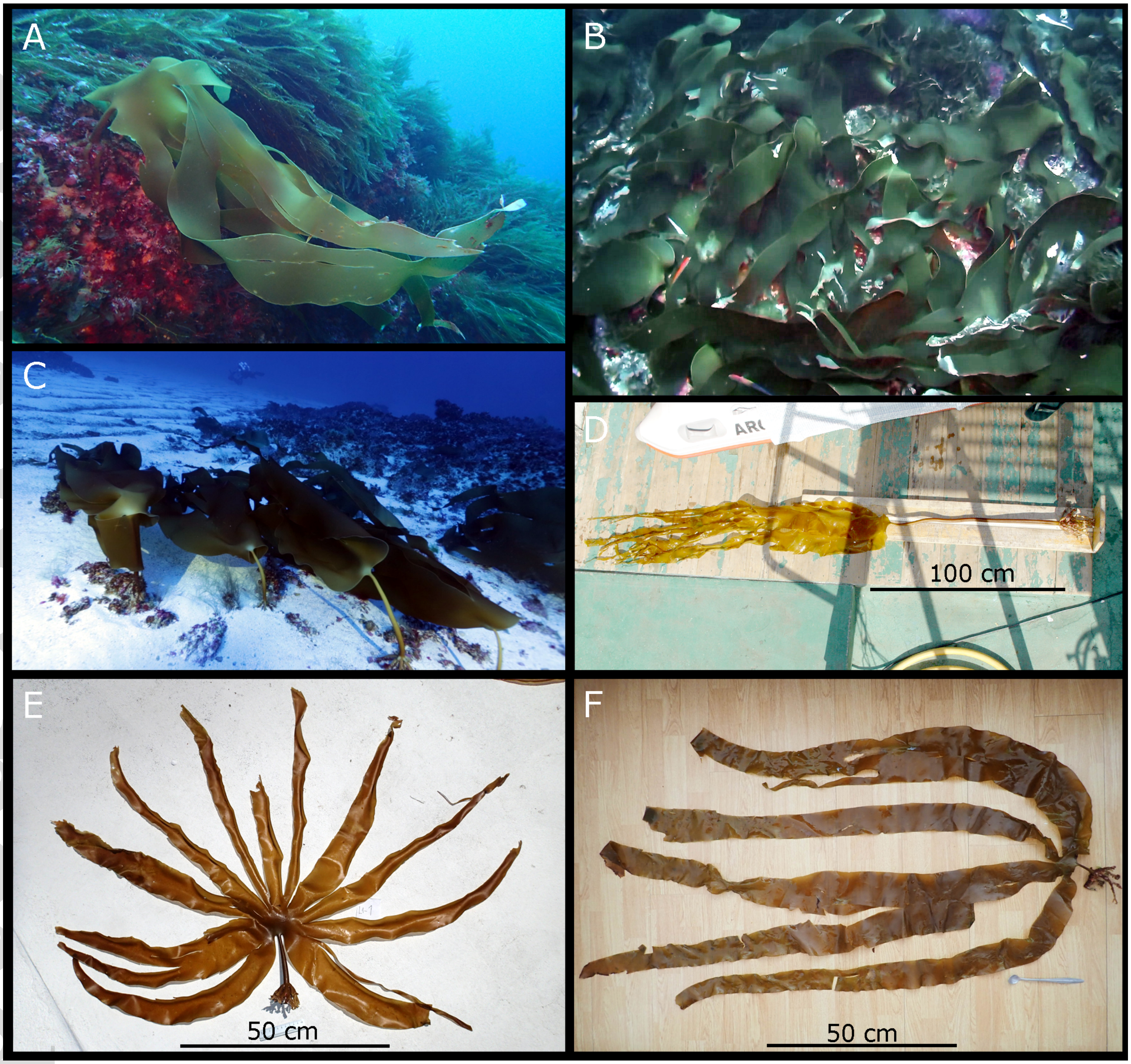

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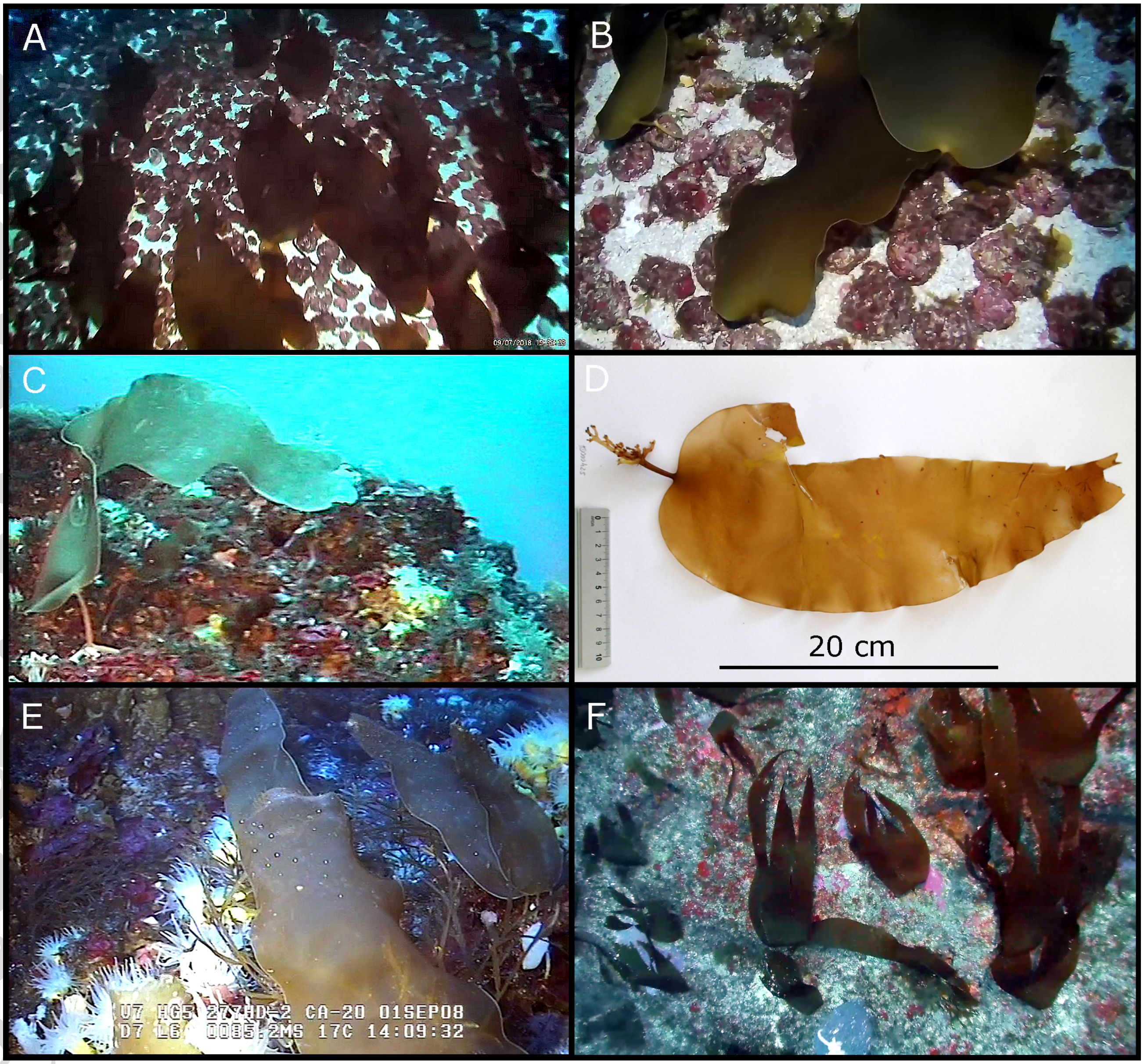

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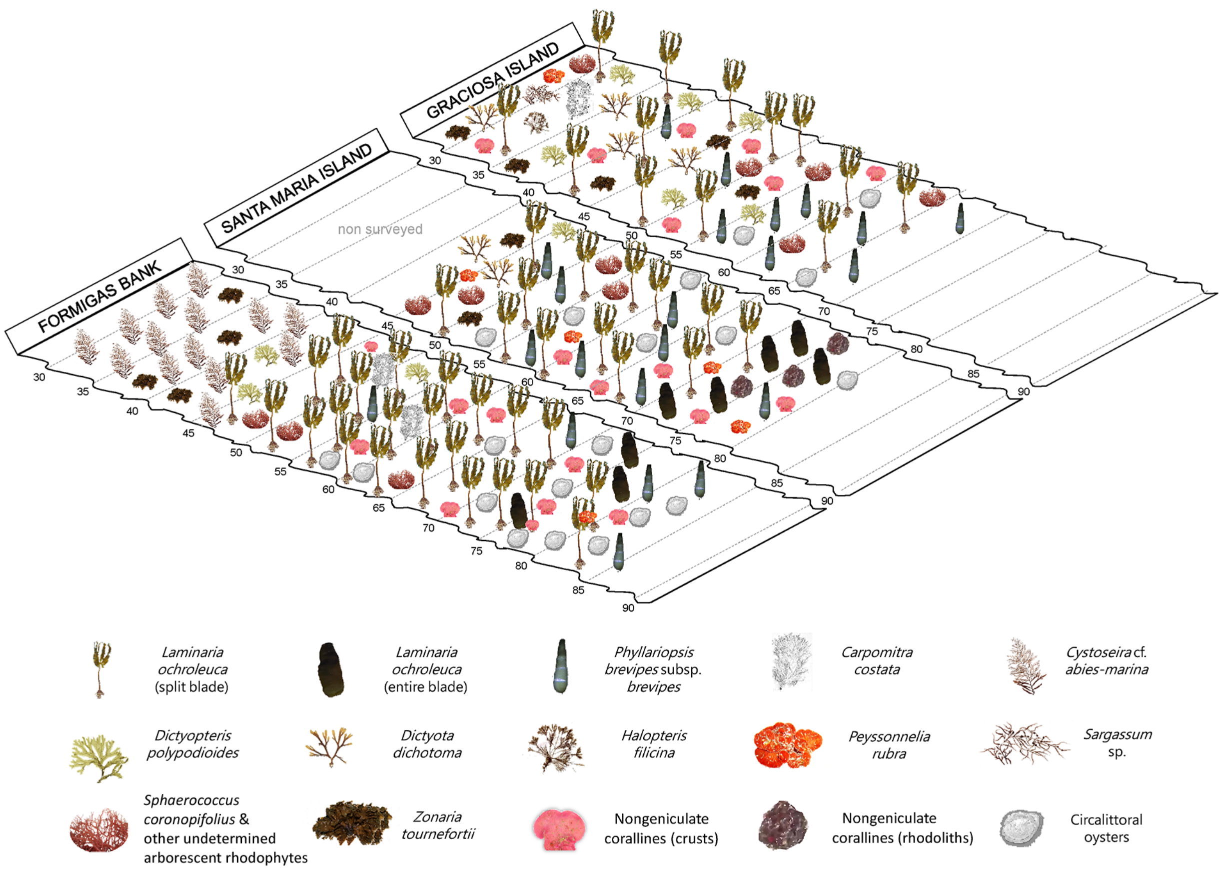

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